이학석사 학위논문

Investigation of co-occurrence patterns of wood-decaying fungi and ants in dead pines of South Korea

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Lupala, Abel

Investigation of co-occurrence patterns of wood-decaying fungi and ants in dead pines of South Korea

Advisor: Professor Young Woon Lim, Ph.D.

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Lupala Abel

School of Biological Sciences

The graduate school

Seoul National University

Abstract

Interaction between fungi and insects such as ants, beetles, wasps and termites inhabiting dead pines has significant ecological implication in the forest as they can decompose wood debris and add nutrients to the soil; however, only scarce information is available regarding the interaction between wood-decaying fungi and ants. Wood-decaying fungi co-occurring with ants in dead pines of South Korea were investigated across 11 localities. A total of 57 pairs of wood-decaying fungi and ants were collected. 30 species of wood-decaying fungi and 14 species of ants were identified based on morphology and molecular analysis. Fungal species belonging to *Trichaptum*, *Xylodon*, *Hyphodontia*, and *Ceriporia* were dominant and co-occurred with common ant species of *Lasius*, *Camponotus*,

Pristomyrmex, and *Crematogaster* across the multiple sampling sites. This study provides a new baseline in unravelling the complex interaction between wood-decaying fungi and ants in forest ecosystems.

Keywords: Ants, Co-occurrence, Decayed pinewood, *Pinus densiflora*, Wood-decaying fungi

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1. Introduction

1.1. Wood-decaying fungi

Wood-decaying fungi are saprotroph and distributed across several orders of class Agaricomycetes (Basidiomycota) (Hibbett et al., 2007). These fungi can decompose wood matters into simple sugars, oligosaccharides and humic substances which are subsequently added to soil (Carlile et al., 2001). Through decomposition of fallen dead wood, these fungi provide habitats for many other organisms and regenerates forests' biodiversity (Sippola et al., 2005; Heilmann-Clausen et al., 2014; Fukasawa et al., 2015). Wood decomposition is a complex ecological process (Herrmann and Bauhus, 2013) which is regulated by different factors: abiotic (e.g. climate conditions) and biotic (e.g. substrate quality) factors and the composition and activity of decomposer fungal communities (Weedon et al., 2009; Liu et al., 2013).

1.2. Wood-decaying fungi and insects' interactions

Habitats and nutrients generated by wood-decaying fungi are sufficient factors to attract various invertebrates (Johansson et al., 2006; Warren and Bradford, 2011). Some of them have also developed symbiotic relationships with these fungi (Hågvar, 1999; Mueller et al., 2005; Schigel, 2011a; Li et al., 2015). Wood boring ambrosia beetles (*Ambrosiodmus* and *Ambrosiophilus*) have a mutualistic

association with the wood degrading fungus, *Flavodon ambrosius* (Hulcr and Stelinski, 2017; Li et al., 2017). Another form of association between fungi and insect is between fungus-cultivating termites (Termitidae, Macrotermitinae) and their obligate mutualistic fungi (Agaricomycetes, Lyophyllaceae, Termitomyces) whereby in this mutualistic association only one termite species is associated to one fungi species (Makonde et al., 2013).

Ants have also exhibited strong co-evolutionary dynamics with fungi (Masiulionis et al., 2014). The most widely known and explored ant-fungus mutualism is between the Attine ants (tribe Attini), best known as "leaf cutter ants" (*Atta* and *Acromyrmex* genera) and their mutualistic fungal cultivars, Leucocoprineae and Pterulaceae, in Southern and Central America and southern parts of USA (Hinkle et al., 1994; Mehdiabadi and Schultz, 2010; Masiulionis et al., 2014). Masiulionis et al (2014) reported that ants can cultivate the fungi in the nest and protect the fungi from alien microorganism such as bacteria and other invading fungi and, in return, these fungi provide nutrients to the ants in the form of specialized inflated hyphal tips called gongylidia. Ants of diverse genera have been observed as common visitors of wood-decaying fungi as well (Lewis and Worthen, 1992; Orr and Charles, 1994; Mueller et al., 2001). Recently, Epps and Penick (2018) scrutinized mushroom visiting ants (*Aphaenogaster* spp.) and reported that these ants with a generalist diet fed on wood-decaying fungus, *Pleurotus ostreatus*.

1.3. Korean pine trees

Coniferous forests have been dominating since 1970 (Kwon., 2016). Out of major conifers such as *Pinus densiflora* (Korean red pine), *Pinus koraiensis* (Korean pine) *Pinus thunbergii* (Black pine), and *Pinus rigida* (Pitch pine), *Pinus densiflora* is the most abundant one in South Korea. This tree is native to Korea, Japan, China, and East Russia (Yu et al.,2004). According to the Korea Forest Service 2016; *P. densiflora* accounts for the 87% of the species in coniferous forests in the country. It has an immense ecological as well as economic importance since it is used for the production of timber as well as playing an important role in many forests' ecosystems (Kwon., 2016).

For the case of dead pines, they are nutrients and habitat source to wood-decaying fungi (Kim et al., 2017). Diverse species of wood-decaying fungi have been reported to be inhabiting dead pines, these include species like *Athelia epiphylla, Fomitopsis pinicola, Gloeophyllum sepiarium, Oligoporus placentus, Phanerochaete filamentosa,* and *Trichaptum abietinum* (Son et al., 2011). These wood-decaying fungi attract insects such as woodborers (Park et al., 2014; Floren et al., 2015) and wasp (Pažoutová and Šrůtka, 2007).

1.4. Objective

Several species of wood-decaying fungi have mutualistic interactions with beetles and wasps (Son et al., 2011; Park et al., 2014., Rajala et al., 2015). In South Korea, where numerous species of wood-decaying fungi and ants such as *Aphaenogaster japonica*, *Camponotus japonicus*, and *Formica japonica* have long been observed to inhabit dead pinewoods (Kwon et al., 2012; Kwon et al., 2013; Kim et al., 2017). However, there has not been a comparable study of mutualistic associations between wood-decaying fungi and ants inhabiting dead pinewoods. To understand their relationship, investigation of their co-occurrence patterns is required first. Therefore, the main objective of this study is to investigate the co-occurrence patterns of wood-decaying fungi and ants in dead pinewoods. Furthermore, to assess which ant-fungi pair have the highest co-occurrence.

2. Materials and methods

2.1. Sampling sites and specimen collection

Sampling of wood-decaying fungi and co-occurring ants on dead pinewoods was conducted between mid-March to September 2018 across 57 sites of 11 locations in Korea (Fig. 1). They were collected only after confirming that (1) wood-decaying fungi and ants were both present on a dead pinewood and (2) an ant nest was found within the dead pinewood. Based on these criteria, samples were not collected when ants simply foraged wood-decaying fungi without a nest underneath. Fungi and ants were collected in pairs after they were confirmed to co-exist in a dead pinewood, either standing or fallen (Fig. 2). All sites were of lower to higher altitude mountainous regions with moderate understory vegetation to completely covered litter layers. In all sites, vegetation was dominated by *Pinus densiflora*.

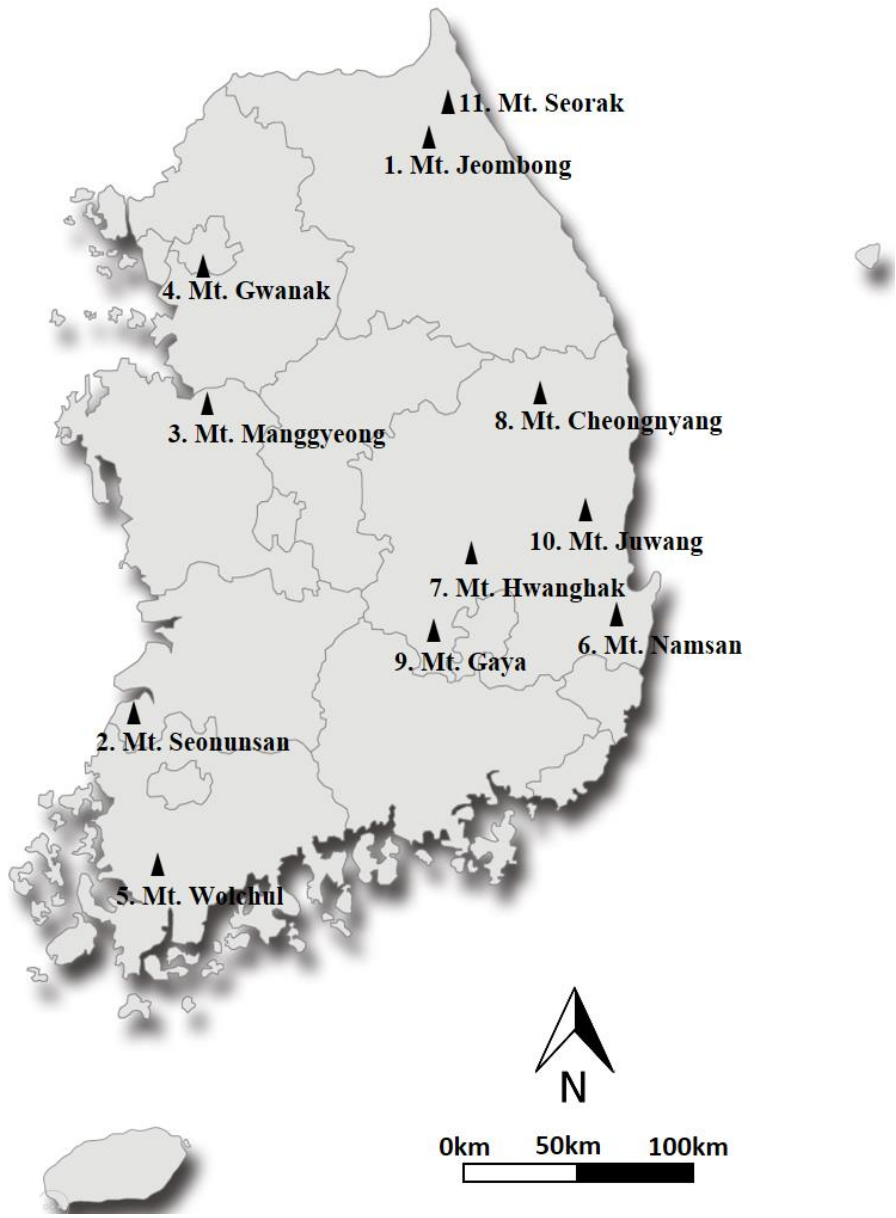

Figure 1. Map of South Korea showing sampling localities.

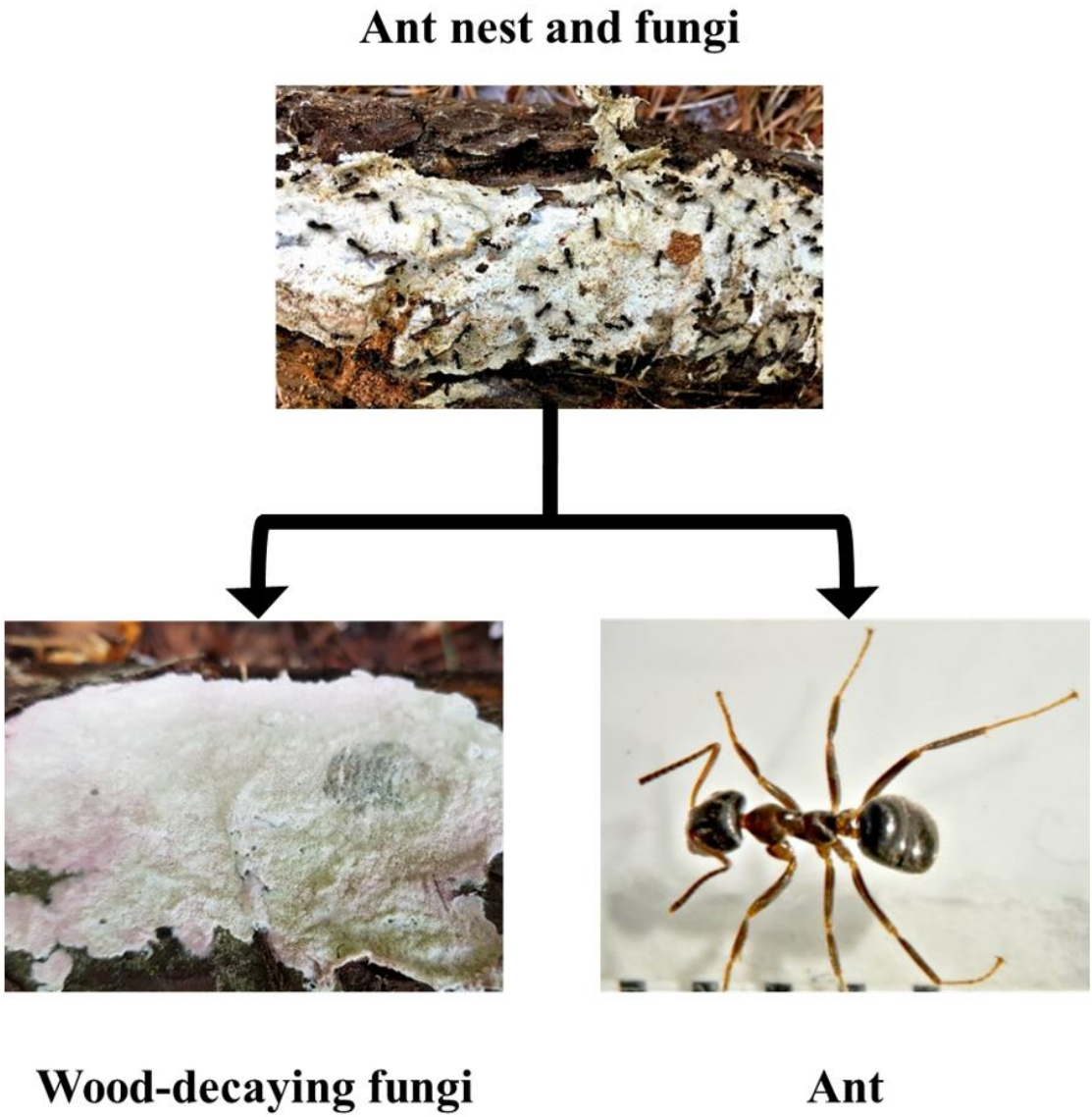

Figure 2. Sampling approach. Collection of co-existing wood –decaying fungi and ants from a dead pine pinewood with ants' nest.

2.1. Fungi collection and identification

Fruiting bodies were collected, dried and deposited in the Seoul National University Fungus Collection (SFC). They were identified via morphological and molecular approaches. Classical methodology was achieved by macro- and micro-morphological observations using taxonomic guides (Largent and Thiers, 1977; Breitenbach and Kränzlin, 1986)

Genomic DNA was extracted from fruiting bodies using a modified Cetyl trimethyl ammonium bromide (CTAB) extraction protocol of Rogers and Bendich (1994). The internal transcribed spacer (ITS) (Fig. 3A) region was amplified using combinations of the forward primers (ITS1F and NSI1) and reverse primers (ITS4B, LB-W, and NLB4) (Table 1) (White et al., 1990; Gardes and Bruns, 1994; Martin and Rygiewicz, 2005; Tedersoo et al., 2008). PCR amplification was performed as described by Park et al. (2013). PCR products were visualized on a 1% agarose gel and purified using the Expin PCR purification kit (GeneAll Biotechnology, Seoul, South Korea). Sanger sequencing was performed at Macrogen (Seoul, South Korea) on an automated DNA sequencer (ABI Prism 3730XL analyzer; Applied Biosystems, Foster City, California) using the aforementioned PCR primers.

Newly generated sequences were proofread and edited using MEGA 5 (Tamura et al., 2011). Molecular identification was conducted with ITS region using BLAST against GenBank database. Species level identification was achieved through the sequence similarity with 98 to 100%. Specimens that had sequence similarity of 95 to 97% or no species information in open database remained at the genus level (Table S1). All sequences were deposited at GenBank under accession number MK992816- MK992868 (Table 2).

2.3. Ants collection and identification

Ants were collected into 1.5 mL Eppendorf tubes containing 70% ethanol by employing hand collection method and transported to the laboratory. Their identification was accomplished by morphological and molecular approaches. For morphological approach, all collected ants were observed under Nikon SMZ1500 stereo microscope and identified according to the taxonomic keys (Japanese Ant Image Database, 2010 (http://ant.edb.miyakyo-u.ac.jp/.); Kwon et al., 2012; Dong, 2017).

Molecular approach was performed as follows. An individual ant was placed in a 1.5 mL Eppendorf tube after the removal of gaster which is known to contain a substance inhibiting the PCR (Feldhaar et al., 2003). Genomic DNA was

extracted by using AccuPrep® Genomic DNA Extraction Kit (Bioneer, Daejeon, South Korea) according to the manufacturer's protocol. For PCR amplification and sequencing, the insect barcode mitochondrial cytochrome c oxidase subunit I (COI) gene was targeted (Fig. 3B) which is the basis of ants' molecular identification (Wilson, 2012). COI was amplified using the primers LCO1490 and HCO2198 (Table 1) (Folmer et al., 1994). PCRs were conducted in the C1000 thermal cycler (Bio-Rad, Hercules, CA, USA) using the AccuPower PCR Premix (Bioneer Co., Daejeon, Korea) in a final volume of 20 μL containing 10 pmol of each primer and 1 μL of DNA under the following conditions: 95°C for 5 min, followed by 35 cycles of 95°C for 40 secs, 45°C for 40 secs, and 72°C for 1 min and a final extension step at 72°C for 10 min.

Purification and sequencing of PCR product was conducted as described in the previous section. As reference sequences of ants native to East Asia are largely unavailable in GenBank, for some ants' specimens, identification was achieved through the BLAST service of the National Institute of Biological Resources (https://species.nibr.go.kr) (Table S2). All ants' sequences were deposited at GenBank under accession number MN010595-MN010641 (Table 3).

Table 1. Information on the primers used for the PCR in this study

Region	Primer	Sequence (5'-3')	Reference
For Fungi			
ITS	NSI1	GATTGAATGGCTTAGTGAGG	Martin and Rygiewicz, 2005
	NLB4	GGATTCTCACCCTCTATGAC	Martin and Rygiewicz, 2005
	ITS1F	CTTGGTCATTTAGAGGAAGTAA	White et al., 1990
	ITS4B	CAGGAGACTTGTACACGGTCC	Gardes and Bruns, 1994
	LB-W	CTTTTCATCTTTCCCTCACGG	Tedersoo et al., 2008
For Ants			
COI	LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al., 1994
	HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al., 1994

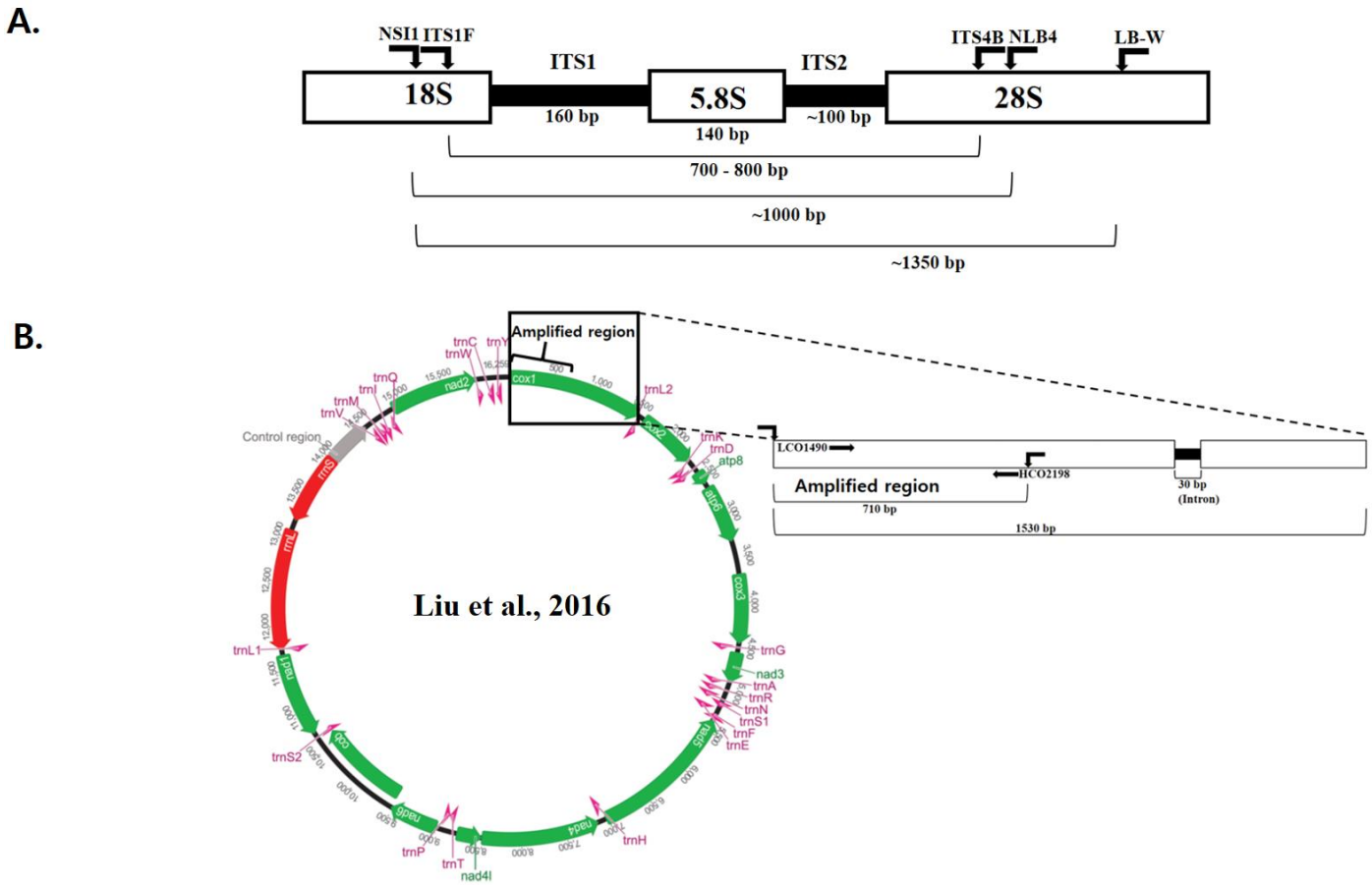

Figure 3. Location of Primers for PCR amplification. A- ITS region, B- COI region.

3. Results

3.1. Wood-decaying fungi inhabiting dead pinewoods

57 wood-decaying fungi co-inhabited with ants were collected from dead pinewoods. They were identified by complementing both morphological and molecular analyses. Five fungal species were first identified morphologically based on their distinctive characteristics followed by molecular confirmation: *Ceriporia nanlingensis*, *Heterobasidion ecrustosum*, *Schizophyllum commune*, *Trichaptum abietinum*, and *Xylodon flaviporus* (Fig. 4). Other species were identified first based on ITS sequence analysis and then confirmed by morphological characters. Forty-eight samples were identified to species level and seven to genus level while two to order level only. A total of 30 species of wood-decaying fungi was confirmed from 57 sites (Table 2).

At the family level, species of Polyporaceae and Schizoporaceae were the most dorminant, followed by Meruliaceae, Rickenellaceae, Tubulicrinaceae, Botryobasidiaceae, and Fomitopsidaceae. The remaining seven families were mostly collected from single sites only (Fig. 5). At the genus level, *Xylodon* and *Trichaptum* were the most dominant genera followed by *Hyphodontia*, *Ceriporia*, *and Botryobasidium* (Fig. 5). In terms of species, *T. abietinum* had the highest collection frequency (9 sites) followed by *Xylodon ovisporus*, *Resinicium*

furfuraceum, and *Hyphodontia pallidula* (each 5 sites). *Ceriporia alachuana* and *Ceriporia naglingensis* were collected from five sites. Species such as *Amylostereum areolatum*, *Heterobasidion ecrustosum*, *Perenniporia koreana*, *Phlebia acanthocystis*, *Postia hirsuta* and *Pseudomerulius aureus* were collected only once (Table 2).

Table 2: List of collected wood-decaying fungi across sampling sites and their Genbank accession numbers

Wood-decaying fungi	Specimen code	Locality	ITS Accession No.
Amylostereaceae			
Amylostereum areolatum	SFC20180314-02	1	MK992817
Atheliaceae			
Athelia epiphylla	SFC20180314-01	1	MK992816
Bondarzewiaceae			
Heterobasidion ecrustosum	SFC20180919-03	11	MK992864
Botryobasidiaceae			
Botryobasidium sp. 1	SFC20180710-21	7	MK992837
Botryobasidium sp. 2	SFC20180609-01	4	MK992824
	SFC20180710-16	6	MK992832
Botryobasidium sp. 3	SFC20180710-22	7	MK992838
Fomitopsidaceae			
Dacryobolus sp. 1	SFC20180907-154	9	MK992862
Dacryobolus sp. 2	SFC20180907-153	9	MK992861
Postia hirsuta	SFC20180822-19	4	MK992857
Hydnodontaceae			
Trechispora confinis	SFC20180710-18	6	MK992834
	SFC20180710-23	7	MK992839
Meruliaceae			
Ceriporia alachuana	SFC20180710-15	6	MK992831
	SFC20180810-01	4	MK992849
	SFC20180810-03	4	MK992851
C. nanlingensis	SFC20180710-17	6	MK992833
	SFC20180822-20	4	MK992858
Phlebia acanthocystis	SFC20180704-91	5	MK992826
P. acerina	SFC20180711-01	8	MK992841
Phanerochaetaceae			
Phlebiopsis gigantea	SFC20180711-02	8	MK992842
Polyporaceae			
Perenniporia koreana	SFC20180719-04	4	MK992847
Trichaptum abietinum	SFC20180531-03	2	MK992820
	SFC20180531-04	2	-
	SFC20180710-12	6	MK992828
	SFC20180710-13	6	MK992829
	SFC20180710-14	6	MK992830
	SFC20180719-05	4	MK992848
	SFC20180822-21	4	-
	SFC20180919-01	11	-

Table 2 Continued

	SFC20180928-35	1	-
Rickenellaceae			
Peniophorella pubera	SFC20180601-02	3	MK992822
P. subpraetermissa	SFC20180719-01	4	MK992844
Resinicium furfuraceum	SFC20180822-18	4	MK992856
	SFC20180907-152	9	MK992860
	SFC20180919-02	11	MK992863
	SFC20180919-06	11	MK992867
	SFC20180929-32	1	MK992868
Schizophyllaceae			
Schizophyllum commune	SFC20180704-92	5	MK992827
Schizoporaceae			
Xylodon chinensis	SFC20180710-20	6	MK992836
	SFC20180818-36	4	MK992854
X. flaviporus	SFC20180710-24	7	MK992840
X. nespori	SFC20180601-03	3	MK992818
	SFC20180822-17	4	MK992819
X. ovisporus	SFC20180531-01	2	MK992846
	SFC20180531-02	2	MK992850
	SFC20180719-03	4	MK992859
	SFC20180810-02	4	MK992823
	SFC20180822-22	4	MK992855
Tapinellaceae			
Pseudomerulius aureus	SFC20180818-35	4	MK992853
Tubulicrinaceae			
Hyphodontia pallidula	SFC20180601-01	3	MK992821
	SFC20180710-19	6	MK992835
	SFC20180711-03	8	MK992843
	SFC20180719-02	4	MK992845
	SFC20180810-04	4	MK992852
Tubulicrinis sp.	SFC20180919-05	11	MK992866
Unidentified family			
Auriculariales sp.	SFC20180919-04	11	MK992865
Hymenochaetales sp.	SFC20180609-02	4	MK992825

Supplementary Table 1. Representative list of molecular identified wood-decaying fungi species and their Genbank matches

Wood-decaying fungi	Specimen code	Closest fungal match (accession number)	Similarity (%)
Amylostereum areolatum	SFC20180314-02	*Amylostereum areolatum* (KX449521)	100
Athelia epiphylla	SFC20180314-01	*Athelia epiphylla* (GU187501)	99
Botryobasidium sp. 1	SFC20180710-21	Cf. *Botryobasidium* (KP814186)	99
Botryobasidium sp. 2	SFC20180609-01	*Botryobasidium* sp. (KY462401)	99
Botryobasidium sp. 3	SFC20180710-22	*Botryobasidium* sp (KY462551)	100
Ceriporia alachuana	SFC20180710-15	*Ceriporia alachuana* (JX623897)	99
Ceriporia nanlingensis	SFC20180822-20	*Ceriporia nanlingensis* (JX623938)	98
Dacryobolus sp. 1	SFC20180907-154	*Dacryobolus* sp. (KJ668557)	99
Dacryobolus sp. 2	SFC20180907-153	Cf. *Dacryobolus* sp. (KP814329)	99
Heterobasidion ecrustosum	SFC20180919-03	*Heterobasidion ecrustosum* (KF218832)	100
Hyphodontia pallidula	SFC20180601-01	*Hyphodontia pallidula* (KP814392)	99
Peniophorella. subpraetermissa	SFC20180719-01	*Peniophorella. subpraetermissa* (NR_119600)	98
Peniophorella pubera	SFC20180601-02	*Peniophorella pubera* （KJ714003)	99

Supplementary Table 1 Continued

Perenniporia koreana	SFC20180719-04	*Perenniporia koreana* (KJ156314)	99
Phlebia acanthocystis	SFC20180704-91	*Phlebia acanthocystis* (KY948767)	99
Phlebia acerina	SFC20180711-01	*Phlebia acerina* (KP135371)	99
Phlebiopsis gigantea	SFC20180711-02	*Phlebiopsis gigantea* (AF087485)	100
Postia hirsute	SFC20180822-19	*Postia hirsuta* (KJ684971)	99
Pseudomerulius aureus	SFC20180818-35	*Pseudomerulius aureus* (GU187534)	99
Resinicium furfuraceum	SFC20180822-18	*Resinicium furfuraceum* (KP814304)	98
Schizophyllum commune	SFC20180704-92	*Schizophyllum commune* (AF249378)	99
Trechispora confinis	SFC20180710-18	*Corticium confine* (MG231494)	98
Trichaptum abietinum	SFC20180710-12	*Trichaptum abietinum* (MF381023)	100
Xylodon chinensis	SFC20180818-36	*Hyphodontia chinensis* (KX857804)	98
Xylodon ovisporus	SFC20180531-02	*Xylodon ovisporus* (MF540764)	99
Xylodon flaviporus	SFC20180710-24	*Schizopora flavipora* (AF145585)	99
Xylodon nespori	SFC20180822-17	*Hyphodontia nespori* (DQ873622)	99
Tubulicrinis sp.	SFC20180919-05	Cf. *Tubulicrinis* sp (KP814266)	95
Auriculariales sp.	SFC20180919-04	*Stypella subgelatinosa* (MK098926)	88
Hymenochaetales sp.	SFC20180609-02	*Tubulicrinis globisporus* (DQ873655)	87

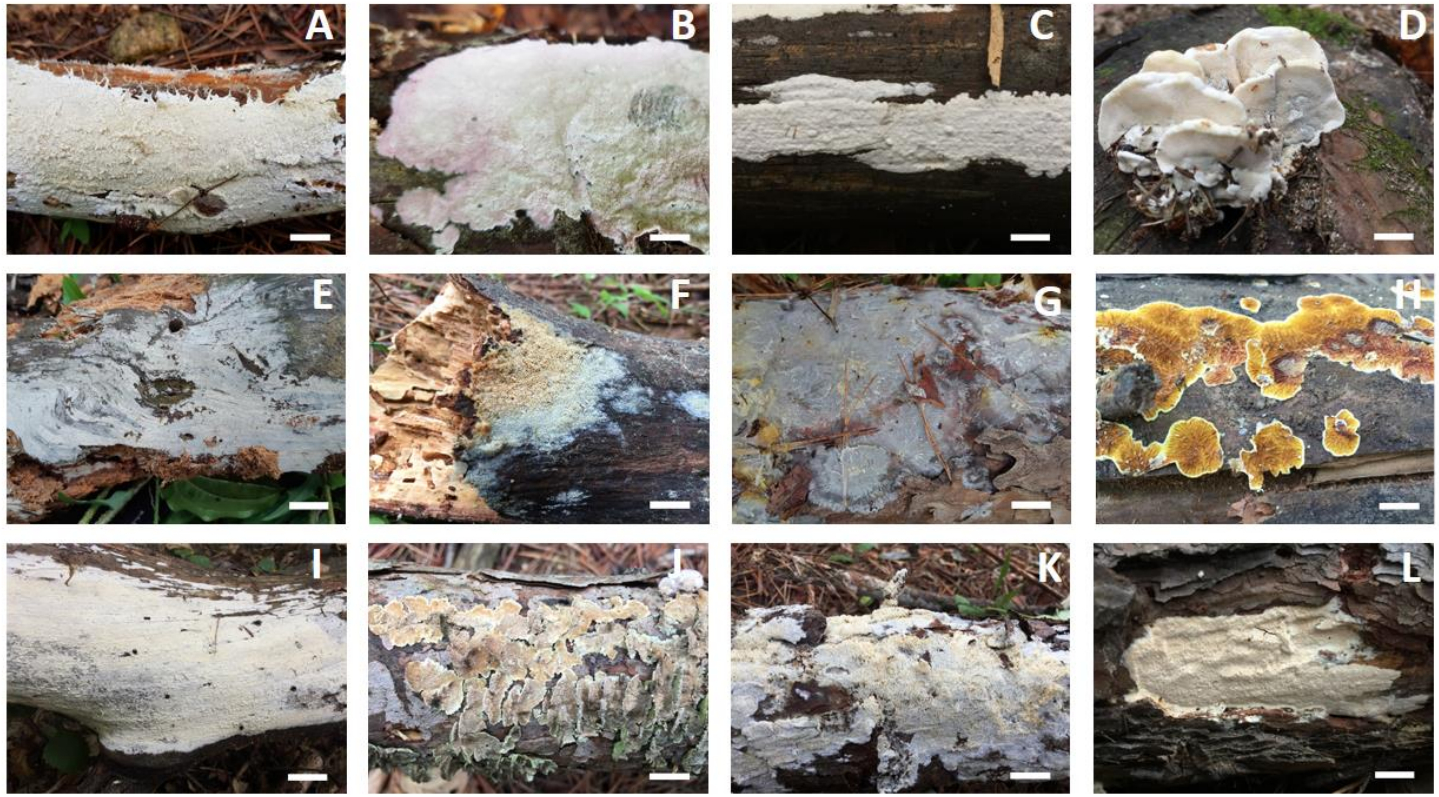

Figure 4. Representative list of collected wood-decaying fungi. **A**- *Ceriporia alachuana*, **B**- *Ceriporia nanlingensis*, **C**- *Dacryobolus* sp. 2, **D**- *Heterobasidion ecrustosum*, **E**- *Hyphodontia pallidula*, **F**- *Phlebia acanthocystis*, **G**- *Phlebia acerina*, **H**- *Pseudomerulius aureus*, **I**- *Resinicium furfuraceum*, **J**- *Trichaptum abietinum*, **K**- *Xylodon chinensis*, **L**- *Xylodon ovisporus*. **Scale bar = 1 cm.**

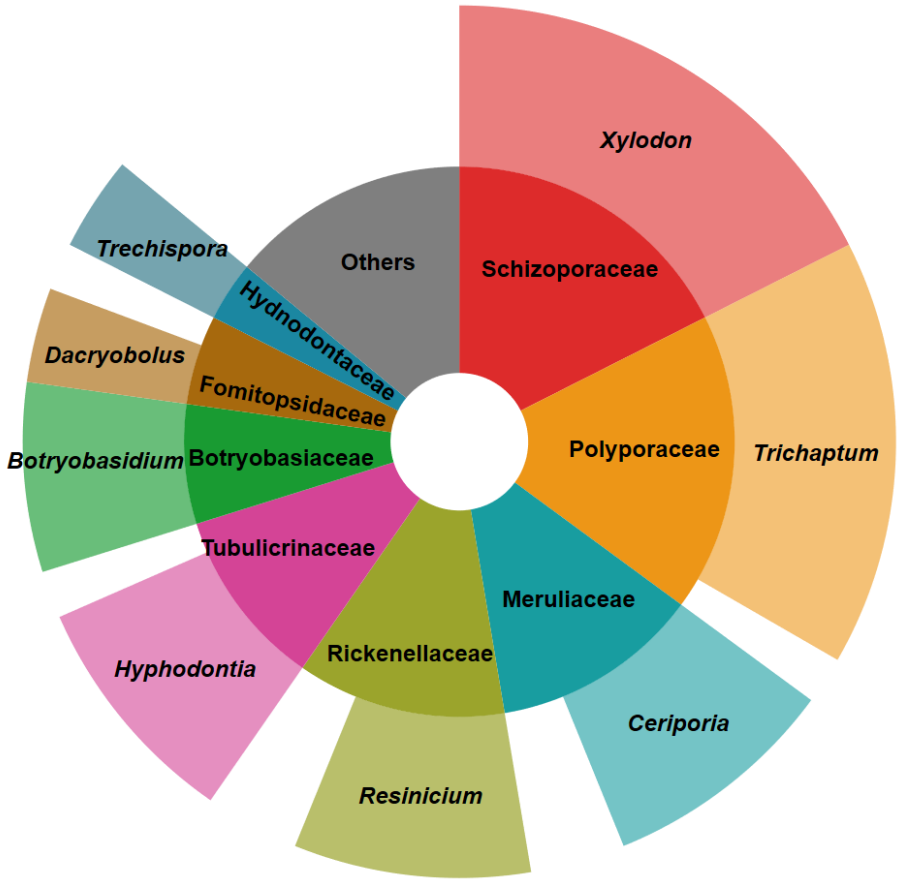

Figure 5. Pie charts of collected Wood-decaying fungi across the sampling sites. Inner cycle-fungal families, Outer cycle-fungal genera.

3.2. Ants nesting in dead pinewoods

Ants collected with wood-decaying fungi were identified as 14 different species (Fig 6) of five tribes, namely Attini, Camponotini, Crematogastrini, Lasiini (Sub-family Formicinae), and Stenammini (Sub-family Myrmicinae) (Table 3, Fig 7). Species frequently observed were *Lasius japonicus* (17 sites) and *Pristomyrmex punctatus* (9 sites), followed by *Crematogaster teranishii* (5 sites), *Pheidole fervida* (5 sites), and *Vollenhovia emeryi* (4 sites). Ants from the genus *Camponotus* had the highest species diversity: *C. atrox*, *C. kiusuensis*, *C. nipponensis*, *C. vitiosus*, and *C. quadrinotatus* (Fig 6). Species of *Aphaenogaster japonica* and *Lasius spathepus* were each collected two times while the least common species *Nylanderia flavipes* and *Polyrhachis lamellidens* were collected once (Table 3).

Table 3: List of collected ants across sampling sites and their Genbank accession numbers

Ants	Specimen code	Locality	COI Accession No.
Attini			
Pheidole fervida	SFC20180907-A03	9	MN010633
	SFC20180919-A03	11	MN010636
	SFC20180818-A01	4	-
	SFC20180531-A03	2	MN010598
	SFC20180531-A04	2	MN010599
Camponotini			
Camponotus atrox	SFC20180314-A01	1	MN010595
	SFC20180929-A01	1	MN010641
	SFC20180928-A01	1	MN010640
C. kiusuensis	SFC20180919-A01	11	MN010634
	SFC20180919-A02	11	MN010635
C. nipponensis	SFC20180810-A04	4	MN010624
	SFC20180822-A03	4	MN010627
	SFC20180818-A02	4	-
C. quadrinotatus	SFC20180822-A01	4	MN010625
C. vitiosus	SFC20180704-A01	5	MN010605
Polyrhachis lamellidens	SFC20180710-A12	7	MN010613
Crematogastrini			
Crematogaster teranishii	SFC20180710-A07	6	-
	SFC20180710-A06	6	-
	SFC20180710-A01	6	MN010606
	SFC20180710-A03	6	-
	SFC20180822-A05	4	MN010629
Pristomyrmex punctatus	SFC20180601-A01	3	MN010600
	SFC20180711-A01	8	MN010615
	SFC20180822-A02	4	MN010626
	SFC20180710-A02	6	MN010607
	SFC20180710-A09	6	MN010610
	SFC20180601-A03	3	MN010602
	SFC20180531-A01	2	MN010596
Vollenhovia emeryi	SFC20180822-A04	4	MN010628
	SFC20180609-A02	4	MN010604
	SFC20180719-A01	4	-
	SFC20180822-A06	4	MN010630

Table 3 Continued

Lasiini			
Lasius japonicus	SFC20180919-A04	11	MN010637
	SFC20180710-A10	7	MN010611
	SFC20180609-A01	4	MN010603
	SFC20180710-A11	7	MN010612
	SFC20180710-A04	6	MN010608
	SFC20180810-A01	4	MN010621
	SFC20180711-A02	8	MN010616
	SFC20180719-A02	4	MN010617
	SFC20180601-A02	3	MN010601
	SFC20180719-A04	4	MN010619
	SFC20180907-A01	9	MN010631
	SFC20180919-A05	11	MN010638
	SFC20180919-A06	11	MN010639
	SFC20180710-A13	7	MN010614
	SFC20180531-A02	2	MN010597
	SFC20180719-A03	4	MN010618
L. spathepus	SFC20180710-A05	6	MN010609
	SFC20180810-A02	4	MN010622
Nylanderia flavipes	SFC20180810-A03	4	MN010623
Stenammini			
Aphaenogaster japonica	SFC20180719-A05	4	MN010620
	SFC20180907-A02	9	MN010632

Supplementary Table 2. **Representative list of molecular identified ant species, their Genbank and NIBR matches**

Ant species	Code number	Closest match (GenBank)	Closest match (NIBR)
Aphaenogaster japonica	SFC20180719-A05	*Aphaenogaster japonica* (99%) KJ920527	*Aphaenogaster japonica* (100%) WBN0014101
Camponotus atrox	SFC20180314-A01	*Camponotus atrox* (100%) KT159775	*Camponotus obscuripes* (100%) WBN0013599
Camponotus kiusuensis	SFC20180919-A01	*Camponotus kiusuensis* (99%) AB019412	*Camponotus kiusuensis* (99%) WBN0013608
Camponotus nipponensis	SFC20180810-A04	*Camponotus* sp (88%) KX347287	*Camponotus nipponensis* (99%) WBN0013611
Campontous quadrinotatus	SFC20180822-A01	*Camponotus quadrinotatus* (98%) AB019414	*Camponotus quadrinotatus* (99%) WBN0013617
Camponotus vitiosus	SFC20180704-A01	*Camponotus vitiosus* (100%) AB019416	-
Crematogaster teranishii	SFC20180710-A01	*Crematogaster* sp (90%) KC501979	*Crematogaster teranishii* (98%) WBN0013993
Lasius japonicus	SFC20180710-A10	*Lasius japonicus* (98%) AB371063	*Lasius japonicus* (94.1%) WBN0013662
Lasius spathepus	SFC20180810-A02	*Lasius fuliginosus* (93%) AY519394	-
Nylanderia flavipes	SFC20180810-A02	*Nylanderia flavipes* (99%) MH754327	-
Pheidole fervida	SFC20180907-A03	*Pheidole fervida* (98%) MH754425	*Pheidole fervida* (99.5%) WBN0014074
Polyrhachis lamellidens	SFC20180710-A12	*Polyrhachis lamellidens* (99%) KM348369	*Polyrhachis lamellidens* (100%) WBN0013700

Supplementary Table 2 Continued

Pristomyrmex punctatus	SFC20180601-A01	*Pristomyrmex punctatus* (99%) AB556946	-
Vollenhovia emeryi	SFC20180822-A04	*Vollenhovia emeryi* (99%) KF815843	*Vollenhovia emeryi* (98%) WBN0013981

-No sequence information

Figure 6. Collected Ants species across sampling sites. **A-** *Aphaenogaster japonica*, **B-** *Camponotus atrox*, **C-** *Camponotus kiusuensis*, **D-** *Camponotus nipponensis*, **E-** *Camponotus quadrinotatus*, **F-** *Camponotus vitiosus* **G-** *Crematogaster teranishii*, **H-** *Lasius japonicus*, **I-** *Lasius spathepus*, **J-** *Nylanderia flavipes*, **K-** *Pheidole fervida*, **L-** *Polyrhachis lamellidens*, **M-** *Pristomyrmex punctatus*, **N-** *Vollenhovia emeryi*. **Scale bar = 1 mm.**

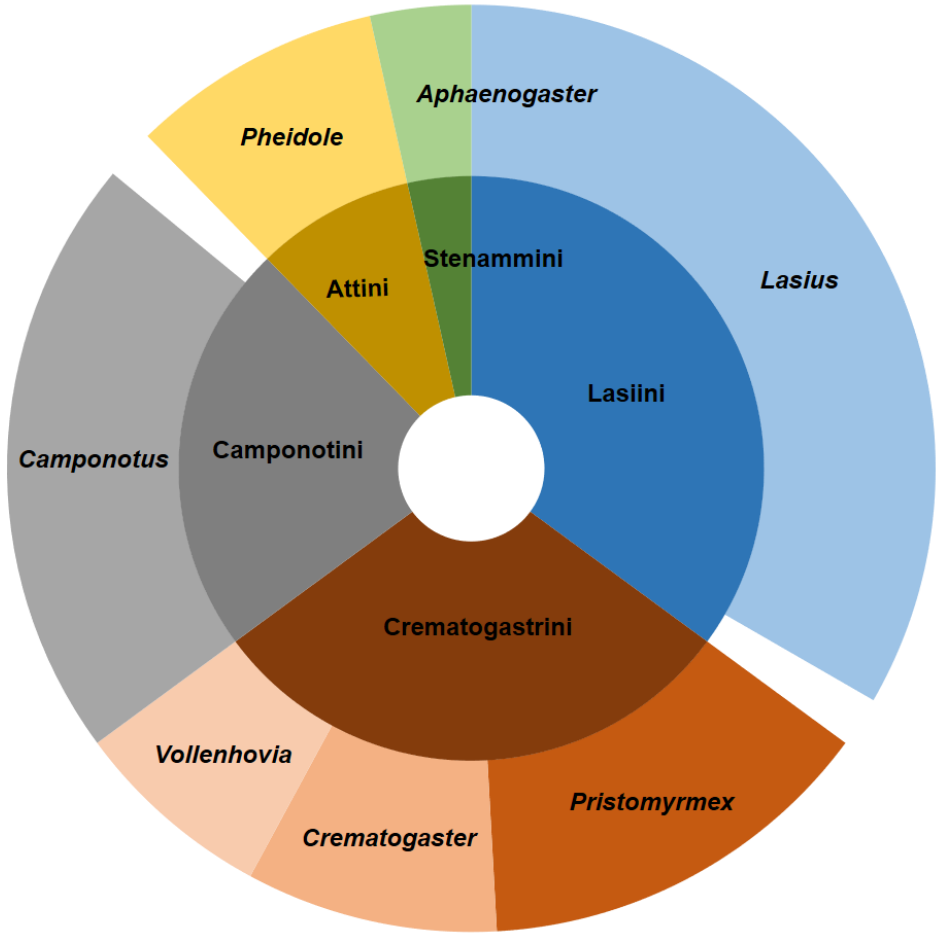

Figure 7. Pie charts of collected ants across the sampling sites. Inner circle ants' tribes, Outer circle ants' genera.

3.3. Co-occurrence patterns of wood-decaying fungi and ants

A total of 57 pairs of wood-decaying fungi and ants were detected from 11 locations. Ants' nests were deep inside dead pinewoods or near the top layer of the dead pine harboring fruiting bodies or mycelia of fungi. At the family level for fungi and tribal level for ants, Polyporaceae co-occurred with all ants' tribes. Meruliaceae, Rickenellaceae, Schizoporaceae and Tubulicrinaceae co-occurred with three tribes Camponotini, Crematograstrini and Lasinii while all Botryobasidiaceae co-occurred with tribe Lasinii only (Fig. 8).

Trichaptum abietinum had the highest number of co-occurrence pairs with numerous species of ants across the sampling sites: three pairs with *Crematogaster teranishii*, two pairs with *Pheidole fervida*, two pairs with *Camponotus* spp. and one pair each with *Aphaenogaster japonica* and *Pristomyrmex punctatus* (Fig. 8). Fungal species of *Xylodon, Botryobasidium* spp, *Ceriporia, Hyphodontia pallidula,* and *Resinicium furfuraceum* followed in terms of co-occurrences pairs with multiple ant species, they showed co-occurrence with *Lasius japonicus* ants. *L. japonicus* ants had the highest number of co-occurrence pairs with wood-decaying fungi across the sampling sites followed by *Pristomyrmex punctatus*, they also co-occurred with multiple fungi species across the sites, the most being three pairs with *Xylodon* species.

Co-occurrence of some wood-decaying fungi and ants was observed by the tendency of ants displaying foraging-like movements on fruiting bodies. Ants from inside the nest and outside surroundings were observed to be displaying these movements on the surface of fruiting bodies. Pairs of wood-decaying fungi and ants involved in this tendency were C*eriporia alachuana* / *Lasius japonicas* (Fig.2), *Heterobasidion ecrustosum* / *Pheidole fervida*, *T. abietinum* / *C. teranishii*, and *X. ovisporus* / *P. punctatus.* Most of the remaining wood-decaying fungi were collected once or twice and co-occurred with commonly observed ants' species across the sites (Fig.8).

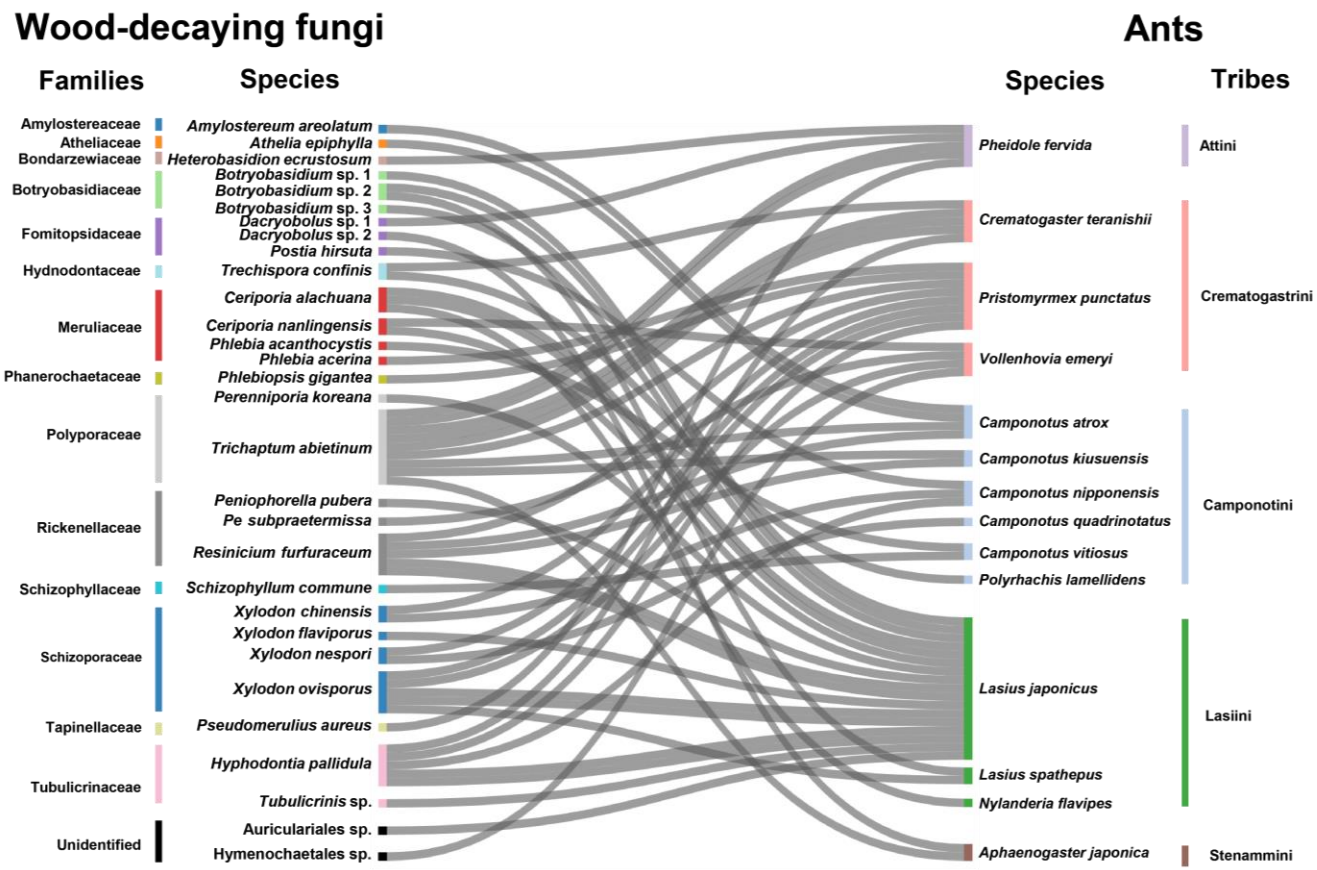

Figure 8. A flow plot of co-occurring pairs of wood-decaying fungi and ants. The left side bars represent families and species of wood-decaying fungi; the right side bars represent the ants' tribes and species. The length of a bar next to the name of a species is proportional to its number of co-occurring pairs.

4. Discussion

Wood-decaying fungi co-occurring with ants in dead pinewoods were surveyed across 11 locations in South Korea. This is the first descriptive study addressing multiple species co-occurrences (wood-decaying fungi and ants) in dead pinewoods of South Korea. Outside South Korea, many studies regarding wood-decaying fungi interactions with insects have only focused on various groups of fungivorous insects; the Czech Republic (Kula et al., 1999), the Fennoscandian countries (Hågvar, 1999; Thunes et al., 2000; Jonsell and Nordlander, 2004; Schigel, 2011b), China (Komonen et al., 2003), Russia (Nikitsky and Schigel, 2004; Krasutskii, 2007), New Zealand (Osawa et al., 2011), Borneo (Yamashita et al., 2015), and Brazil (Valer et al., 2016).

Wood-decaying fungi are key players in forest ecosystems because of their ability to decompose dead wood, recycling nutrients and initiating a successional dynamic for saproxylic arthropods (Jönsson et al.,2008; Lonsdale et al.,2008). A list of collected wood-decaying fungi from decaying pinewoods in this study was consistent with the relevant previous studies in Korea (Kim et al., 2009; Jang et al.,2014; Jang et al., 2016; Kim et al., 2017) and also outside Korea (Kubartová et al.,2012; Walker et al., 2014; Ottosson et al., 2015; Fukasawa and Matsuoka, 2015). *Athelia epiphylla* and *Schizophyllum commune* are known to be exclusive to deciduous trees (Allen et al 2000; Takemoto et al., 2010), but rarely reported from

coniferous trees such as pine (Kim et al., 2009). *Trichaptum abietinum*, which was frequently observed on pinewoods, is known as the first colonizer on dead pinewoods in many forests (Weslien et al., 2011). *Hyphodontia* and *Xylodon* (specifically *Xylodon ovisporus*) were also dominant on decaying pinewoods across the sampling sites and have been reported to be common in deciduous forests, as well (Gafforov et al., 2017). *Ceriporia* species which can cause decaying of both deciduous and coniferous wood were also common (Wulandari et al., 2018). *Ceriporia alachuana* and *Ceriporia nanlingensis* are commonly isolated from pinewood (Dai, 2012). Other observed species were all frequently found from decaying pinewood (Lee and Jung, 2006; Wooding et al., 2013; Jang et al 2016).

Ants associated with the occurrence of wood-decaying fungi in this study were 14 species. These species were all reported in previous ants' communities' surveys in South Korea (Kim and Lyu, 2012; Kwon et al.,2013, 2014a, 2014b; Kwon, 2015a; Kwon, 2015b; Kwon and Lee, 2015; Kwon, 2016). *Lasius japonicus* was the most frequently detected ant species in this study. It is frequently found in Korean forests and dead pinewood is one of its preferred nesting place (Kwon and Lee, 2015). The least collected ant species in this study, *Nylanderia flavipes* also has been reported as one of the most common ant species in Korean pine forests (Kwon and Lee, 2015). Remaining species such as *Aphaenogaster japonica*, *Camponotus* spp., *Crematogaster teranishi*, and *Pheidole fervida* have been

previously observed to be nesting inside decayed pinewood (Kwon et al., 2014b; Kwon, 2016).

For some wood-decaying fungi, interaction with insects is crucial for their establishment and colonization in dead woods (Strid et al., 2014). Insects such as bark beetles and wasps are one of the key players in dispersal of fungal spores to new dead trees (Floren et al., 2015). Bark beetles are usually the first species to colonize newly dead or dying tree and feed on the nutrient-rich phloem (Ejrnæs et al., 2006; Son et al., 2011; Weslien et al., 2011), followed by wood-decaying fungi that colonize broken or cut stems or scars in the bark (Son et al., 2011). Most of the wood-decaying fungi found in this study were previously reported to be associated with beetles and wasps (Ševčík, 2003; Persson et al., 2011; Son et al., 2011; Olatinwo et al., 2013; Strid et al., 2014). *Amylostereum areolatum* and *Athelia epiphylla* are well known decaying fungi to have an interaction with wasp and beetles, respectively (Rajala et al., 2015; Seibold et al., 2019).

Although with limited sampling, results from this study showed that various wood-decaying fungi were co-occurring with ants on dead pines. Ants were also observed to display foraging like movement on basidiocarps.

Foraging activities of *Camponotus* species on basidiocarp of unnamed wood-decaying fungi have been reported previously (Orr and Charles, 1994). *Aphaenogaster* ants also visited and harvested pieces of basidiocarps of the genera

Amanita, *Armillariella*, *Marasmiellus*, and *Russula* (Carroll et al., 1981). Most recent findings showed laboratory and field evidences of interaction between wood-decaying fungi (*Laetiporus* and *Pleurotus ostreatus*) and ants *Aphaenogaster* species (Epps et al., 2018).

Decomposing dead pinewood provides essential habitat for various ants, beetles, and wood-decaying fungi (Warren and Bradford, 2011). Since many wood-decaying fungi are associated with various beetles and wasps, it raises the question whether they also have any sort of association with ants. It is challenging to prove the specific relationship of wood-decaying fungi and co-occurring ants because there can be various explanations for such co-occurrences: e.g., i) wood-decaying fungi may have a specific relationship with ants, ii) accidental co-occurrences, and iii) beetles may carry fungal spores and then ants use basidiocarps or mycelia as food source, etc. More research is needed to uncover such relationship.

5. Conclusions

This study provides a new baseline in unravelling the complex interaction between wood-decaying fungi and ants in forest ecosystems. Both wood-decaying fungi and ants are important in providing nutrients to the soil through decomposition of wood debris; yet, much is not known on how they interact with each other at this specific niche of dead pinewood. Though this study is limited with small sample size, it nonetheless showed diverse patterns of co-occurrence between wood-decaying fungi and ants. Based on observations, future studies are needed to answer the following questions: Is there any specific interaction between wood-decaying fungi and ants? Do the ants participate in dispersal of their spores? If so, how do the mechanisms happened by functional way?

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7. Abstract in Korean

한국의 죽은 소나무에서 공동 발생하는 목재부후균과 개미에 대한 고찰

루팔라

생명과학부 대학원

서울대학교

초 록

죽은 소나무에 서식하는 개미, 딱정벌레, 말벌, 흰개미와 같은 곤충과 균류의 상호작용은 목재 잔해를 분해하고 분해 산물을 토양으로 환원할 수 있기 때문에 숲에서 생태학적으로 중요한 의미를 갖는다. 그러나 목재부후균과 개미 사이의 상호작용에 관한 정보는 매우 부족하다. 이 연구에서는 국내의 죽은 소나무에서 개미와 함께 발견되는 목재부후균을 조사하였으며, 각기 다른 여러 지역에서 총 57 쌍의 목재 부후균과 개미가 채집되었다. 형태 및 분자 동정에 근거하여 총 30 종의 목재부후균과 14 종의 개미가 확인되었다. *Trichaptum* 속, *Xylodon* 속, *Hyphodontia* 속, *Ceriporia* 속에 속한 균류가 우점하였으며, 여러 채집지에서 *Lasius* 속, *Camponotus* 속, *Pristomyrmex* 속,

Crematogaster 속에 속한 비교적 흔한 개미와 함께 채집되었다. 이 연구는 산림 생태계에서 목재부후균과 개미 사이의 복잡한 상호작용을 이해하기 위한 새로운 단초를 제시하였다 .

주요어: 개미, 공발생(共發生), 부식된 소나무, 적송

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